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The Nutrition of *Salmonella*

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A number of strains of *Salmonella* were studied to determine their nutritional requirements in an attempt to find material for genetic analysis (Lederberg and Tatum, 1946). A summary of these findings will be given here.

The majority of strains are capable of growth on a simple synthetic medium (Gray and Tatum, 1944) containing glucose, salts and asparagine, as listed in Table I. All strains were first tested to determine whether they could develop optimally on this medium, by taking very small inocula from slant cultures of the various strains into 10 ml. The strains which failed to show rapid growth were tested further to determine the supplementation that was required, using previously described techniques (*cf.* Burkholder, 1943).

Individual strains of which the requirements have been determined are listed in Table II.

Hohn and Herrmann (1936) have attempted to classify the *Salmonella* group according to growth in a synthetic medium. The strains were designated as "ammonstark" and "ammonschwach," respectively. It is likely that the basis of this distinction is not the ability to assimilate ammonia, but the ability to synthesize specific growth factors such as those listed in Table II. The utility of such a classification has been questioned by Edwards and Bruner (1940) and Kauffmann (1941) who found considerable nutritional variation among strains of similar serological and epidermiological behavior.

From the work of Gray and Tatum (1944) and Roepke *et al.* (1944) on *Escherichia coli*, and of Beadle and Tatum (1941) on *Neurospora*, it is likely that growth factor deficiencies of bacteria are the result of mutations of genes controlling specific steps in

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biochemical syntheses. For example, the ability of ornithine and citrulline to replace arginine in the growth of *S. enteritidis* (S45) suggests that these compounds are biosynthetic precursors of arginine, and that the formation of ornithine is prevented in this organism by the mutation of a gene controlling its synthesis (Srb and Horowitz, 1944).

TABLE I

Salmonella Types With No Growth Factor Deficiencies

Type	Number of strains tested	Type	Number of strains tested
*S. paratyphi A	5	S. montevideo	6
* typhi-murium*	19	tennessee	1
san diego	1	georgia	1
reading	1	newport	11
derby	5	oregon	1
essen	1	glostrup	1
budapest	1	düsseldorf	1
california	1	amherstiana	1
brandenburg	1	* enteritidis	9
abortus equi	1	dar-es-salaam	1
abortus bovis	2	panama	3
bredeney	1	javiana	1
* cholerae suis	4	london	1
thompson	1	give	1
oranienburg	4	uganda	1
bareilly	4	anatis	2
hartford	1	münster	1
zanzibar	1	onderstepoort	1
meleagridis	1	hvittingfoss	1
infantis	1	gaminara	1
pueris	1	kirkee	1
newington	1	kentucky	1
new-brunswick	1	minnesota	1
illinois	1	tel-aviv	1
senftenberg	1	ballerup	1
aberdeen	1	urbana	1
rubislaw	1	inverness	1
poona	1	adelaide	1
carrau	1	italiana	1
sendai	1 (slow on minimal)	champaign	1

Types marked * also have representatives with growth factor requirements. *Cf.* Table II.

TABLE II

Deficient Strains of Salmonella

Strain	Requirements
*S1 paratyphi A	methionine, tryptophan (or indole)
*S42 paratyphi A	tryptophan (or indole)
S51 paratyphi B	proline
*S4 cholerae suis	methionine
*S55 cholerae suis	tryptophan (or indole), cystine
*S56 cholerae suis	biotin, tyrosine
S36 gallinarum	thiamine
S37 dublin	thiamine
*S45 enteritidis	arginine (replaceable by ornithine or citrulline)
S12 pullorum	leucine, cystine
S14 pullorum	leucine, cystine, methionine
*S61 typhi-murium, IV-variant	methionine
S. paratyphi A	not determined
S. paratyphi B	not determined
S. typhi suis	not determined
S. abortus ovis	not determined

Types marked * also have representatives without growth factor requirements. *Cf.* Table I.

The persistence in the natural populations of these organisms of growth factor requirements, of mutational origin, can hardly be regarded as an accident. In the laboratory the loss of these requirements, presumably by reverse-mutation, is a relatively frequent occurrence both in *Salmonella* strains and in nutritional mutants of *E. coli* (Ryan and Lederberg). By plating large numbers of cells into agar lacking the specific growth factors, one may select for "reverted" types of *S. enteritidis* (S45) which are capable of synthesizing ornithine, of *S. cholerae suis* (S55) capable of synthesizing cystine, and so forth. To account for the maintenance of these requirements, it seems necessary to assume that the deficient types found in nature have a selective advantage over reverted types. An illustration of this sort of competition in laboratory populations has been found in *Neurospora* (Ryan and Lederberg, 1946).

It would be dangerous to draw conclusions concerning the evolutionary development of the *Salmonella* group from their nutritional behavior because of the demonstrated lability of these characters. The reversibility of requirements indicates, however, that the ability to synthesize growth factors is the more primitive stage (*cf.* Lwoff, 1942). It is unlikely that the function of synthesizing a required metabolite, could be so readily evolved, *de novo*. One may conclude, therefore, that nutritional reversion represents the reacquisition of a function, the gene for which had been only partially impaired. The common occurrence of reversible requirements suggests that there is also other latent genic material which, although propagated from generation to generation, has no demonstrable function. Such genes are perhaps available for the divergent mutations which are required for evolutionary progress.

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Summary

The nutrition of a variety of *Salmonella* cultures has been studied. The majority have no growth factor requirements; other strains requiring various amino acids and vitamins are described.

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